Impact of climate and moonlight on a venomous mammal, the Javan slow loris (*Nycticebus javanicus* Geoffroy, 1812)

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Abstract

Predation pressure, food availability, and activity may be affected by level of moonlight and climatic conditions. While many nocturnal mammals reduce activity at high lunar illumination to avoid predators (lunarphobia), most visually-oriented nocturnal primates and birds increase activity in bright nights (lunarphilia) to improve foraging efficiency. Similarly, weather conditions may influence activity level and foraging ability. We examined the response of Javan slow lorises (*Nycticebus javanicus* Geoffroy, 1812) to moonlight and temperature. We radio-tracked 12 animals in West Java, Indonesia, over 1.5 years, resulting in over 600 hours direct observations. We collected behavioural and environmental data including lunar illumination, number of human observers, and climatic factors, and 185 camera trap nights on potential predators. *N. javanicus* reduced active behaviours in bright nights. Although this might be interpreted as a predator avoidance strategy, animals remained active when more observers were present. We did not find the same effect of lunar illumination on two potential predators. We detected an interactive effect of minimum temperature and moonlight, e.g. in bright nights slow lorises only reduce activity when it is cold. Slow lorises also were more active in higher humidity and when it was cloudy, whereas potential predators were equally active across conditions. As slow lorises are well-adapted to avoid/defend predators by crypsis, mimicry and the possession of venom, we argue that lunarphobia may be due to prey availability. In bright nights that are cold, the combined effects of high luminosity and low temperature favour reduced activity and even torpor. We conclude that Javan slow lorises are lunarphobic – just as the majority of mammals.

Contents

Introduction

To secure maintenance, survival and reproduction, animals adapt their behaviour to various factors, such as climate, availability of resources, competition, predation, luminosity, habitat fragmentation, and anthropogenic disturbance (Kappeler and Erkert, 2003; Beier *et al.*, 2006; Donati and Borgognini-Tarli, 2006). According to optimal foraging theory, animal behaviour can be seen as a trade-off between the risk of being preyed upon and the fitness gained from foraging (Charnov, 1976). Perceived predation risk assessed through indirect cues that correlate with the probability of encountering a predator may shape an animal's behaviour (Vasquez, 1994; Thorson *et al.*, 1998; Orrock *et al.*, 2004).

55 One of the indirect cues that animals use to assess predation risk is moonlight (Beier *et al.*, 2006;
56 Upham and Haffner, 2013). Most mammals decrease activity or change habitat choice with
57 increasing lunar illumination (lunarphobia) (Price *et al.*, 1984; Hecker *et al.*, 1999; Horning and
58 Trillmuch, 1999; Nash, 2007; Penteriani et al., 2011; Prugh and Golden, 2014; Saldana-Vásquez and
59 Munguía-Rosas 2013) to be more concealed from predators. Some species increase their activity in
60 brighter nights (lunarphilia) due to prey availability, higher foraging efficiency, or better visual
61 detection of predators (Table 1) (Horning and Trillmich, 1999; Packer *et al*., 2011; Prugh and Golden,
62 2014). Whether a species is lunarphobic or lunarphilic depends on the primary sensory system (e.g.
63 visual acuity), phylogenetic relatedness, and habitat cover (Hecker *et al.*, 1999; Michalski and Norris,
64 2011; Saldana-Vásquez and Munguía-Rosas, 2013; Prugh and Golden, 2014). Primates, for instance,
65 are highly visually oriented (Gursky, 2003; Bearder *et al.*, 2006) and are mainly lunarphilic, as
66 opposed to rodents, lagomorphs carnivores and bats, which are largely lunarphobic (Prugh and
67 Golden, 2014). Additionally to lunarphobia and lunarphilia, some species are lunarneutral, although
68 the methods chosen may have an influence whether a certain reaction is found (Nash, 2007;
69 Penteriani *et al.*, 2011). The trade-offs regarding the reaction towards moonlight may vary between
70 species, and even local populations (Lang *et al.*, 2005; Saldana-Vásquez and Munguía-Rosas, 2013).

71

72 A second cue that may affect animal activity is weather condition, causing variation in the detection
73 of prey and predators, and influencing thermoregulation (Hanya, 2004). In general, low temperature
74 causes animals – prey and predator species - to decrease activity to conserve energy. Low
75 temperature especially affects the activity of poikilotherm species like amphibians or arthropods
76 (Fitzgerald and Bider, 1974; Fadamiro and Wyatt, 1995) but also homeotherm species that may
77 decrease activity, employ social and postural thermoregulation (Donati *et al.*, 2011), or go into
78 torpor or hibernation (Schmid, 2000; Smit *et al.*, 2001; Dausmann *et al.*, 2005; Schuelke and Ostner,
79 2007). Humidity and precipitation may affect animal activity. Strong rain or wind generally decrease
80 insect availability and can impede the ability of predators to detect prey (Vickery and Bider, 1981;

Thies *et al.*, 2006). Some animals are more active in high humidity and precipitation due to food availability or physiological needs (amphibians: Fitzgerald and Bider, 1974; rodents: Orrock *et al.*, 2004; insects: Fadamiro and Wyatt, 1995; arthropods: Skutelsky, 1996), some decrease activity due to energetic constraints (primates: Donati and Borgognini-Tarli, 2006; bats: Voigt *et al.*, 2011).

Asian lorises (Lorisinae) are characterized by a suite of morphological traits that makes them sensitive to predators, foraging and temperature. Both slow (*Nycticebus*) and slender (*Loris*) lorises are arboreal slow climbers (Crompton *et al.*, 1993), and rely on crypsis to avoid predators. *Nycticebus* is venomous, a trait that has been attributed to predator defence (Alterman, 1995; Nekaris *et al.*, 2013), which might also affect its activity. High susceptibility to predators suggests that lorises would more likely be lunarphobic. Wild data, however, do not follow a consistent pattern. Wild *Loris tardigradus* (Linnaeus, 1758) tended to lower activity in bright nights, although this was not significantly different from dark night behaviour; they rested, groomed more and whistled more frequently during bright nights, but not significantly suggesting lunarneutrality (Bernede, 2009). Although in general, grey slender lorises were lunarneutral, *L. lydekkerianus* (Cabrera, 1908) were in some aspects lunarphilic (Bearder *et al.*, 2001; 2006), whistling more in bright nights, and foraging more for energy-rich insects (Bearder *et al.*, 2001). Infants of *L. lydekkerianus* however, sought more habitat cover in bright nights, possibly as predator avoidance strategy, indicating lunarphobia for this age class (Bearder *et al.*, 2001). In Cambodia, the pygmy loris (*Nycticebus pygmaeus* Bonhote, 1907) was lunarphobic, especially in cold nights (Starr *et al.*, 2012). During surveys of the Javan slow loris (*N. javanicus* Geoffroy, 1812) lunar neutrality was suggested in that moonlight had no impact on detectability of the species (Nekaris *et al.*, 2014). Captive greater slow lorises (*N. coucang* Boddaert, 1785) reduced activity with higher illumination (Trent, 1977).

It is notable that in the single wild study with clear evidence of lunarphobia, Starr *et al.* (2012) found that decrease in activity was heightened during low temperatures. Lorisines have low metabolic rates, good fur insulation, and possess extensive vascular *retia mirabilia* that help them to stay inactive for prolonged periods (Whittow *et al.*, 1977; Mueller, 1979). Most notably, *Nycticebus spp.* enter torpor for hours or days in cold temperatures (Nekaris and Bearder, 2011). Starr *et al.* (2012) proposed that the combined risk of both predation and heat loss outweigh the benefits of being active, and that temperature should be considered in further discussions of loris activity.

The Javan slow loris (*Nycticebus javanicus*), endemic to Java, Indonesia (Nekaris and Bearder, 2011), weighs around 1 kg, is known to go into torpor, and occurs at least up to 1800m ASL (Nekaris *et al.*, 2014; Nekaris and Rode-Margono, unpub. data). Indeed, much of the forest left on Java where slow lorises are found is at altitudes above 1000 m (Nekaris *et al.*, 2014; Voskamp *et al.*, 2014). We thus examined the effect of lunar illumination and temperature on activity of the Javan slow loris at a high altitude site replete with numerous potential predators. We also examined microhabitat use in the light of understanding predator perception.

Methods

We conducted our study on the foothills of the active volcano Papandayan in West Java. The site was located at altitudes ranging from 800 m - 1800 m asl, ranging into Zones that are in Java classified as Sub-montane (1200 m – 1800 m asl) and Montane Zones (1600 m - 2400 m asl); at altitudes above 1500 m asl, ground frost can occur (Nijman, 2013). The research site was located at S7°6’6 - 7°7’0 and E 107°46’0 - 107°46’5 and consisted of a mosaic-like landscape with forest and bamboo fragments (*talun*) and agricultural fields. Average temperature is relatively constant, but precipitation varies during the year (Figure 1), and daily minimum temperature ranges between 10.4°C and 20.7°C.

We captured 12 animals by hand, took morphometric measurements, fitted a radio collar (ca. 17 g, Biotrack, UK) and released the animal at the capture site. From April 2012 to June 2013, we followed animals in two shifts from 18:00 h to 0:00 h and 00:00 h to 6:00 h (Wiens and Zitzmann, 2003) using antenna (6 and 8 element flexible Yagi antenna, Biotrack, UK) and receiver (R1000, Communication Specialists, US). We used instantaneous focal animal sampling with 5-minute intervals for behaviour and habitat data collection (Altmann, 1974). We followed the ethogram of Moore (2012) and grouped resting and sleeping into the category "not active" and all other behaviours except other into "active". We recorded the heights of the animal and used tree. Assuming that a higher position in the tree provides more concealment by the canopy, we used the relative height (height of the animal divided by height of the tree) of the animal's used tree as an indication of safety. We recorded any sighting of potential nocturnal predators, including common palm civets (*Paradoxurus hermaphrodites* Pallas, 1777) and leopard cats (*Prionailurus bengalensis* Kerr, 1792). Additionally, we had one to four camera traps (Cuddeback Attack IR; Bushnell Trophy cam night vision) installed in 185 nights (304 individual camera trap nights). Cameras were installed about 50 cm above the ground in relatively dense forest or bamboo patches with undergrowth, located within home ranges of radio-tracked slow lorises. With a TFA Nexus weather (TFA Dostmann, Germany) station located at our basecamp, we collected data on temperature, humidity, rain and wind, with one data point every hour. We calculated minimum temperature of the night and rain over the last 24 hours. We estimated cloud cover in the field to the nearest 10 %. Luminosity was recorded using the exact percentage of the moon illuminated when above the horizon, using the programme MOONDV version 1 (Thomas, 1998). When below the horizon an illumination of 0 was recorded.

Statistical analysis

To guarantee independence of the data we used only every 6th data point of our dataset, yielding single observations of the same individuals that were at least one hour apart. We excluded the first and last hour of the night (18:00 to 19:00 and 05:00 to 06:00) to ensure that astronomical twilight is excluded from the data. Astronomical twilight is defined as the moon being 18° below the horizon (Erkert, 2003). Twilight effects on activity may result in peaks at dawn and dusk and an overrepresentation of certain behaviours usually performed in these periods (Bearder *et al.*, 2001; 2006; Erkert and Cramer, 2006). We applied a logistic regression model due to the non-normal distribution of our data (c.f. Starr *et al.*, 2012). We used the binary dependent variable "active" and "not active" (Field 2009). The predictor variables were sex, number of observers, luminosity, minimum nightly temperature, average humidity per night, wind, cloud cover, rain per hour and relative height of slow loris. Humans can be seen as predators (Charles-Dominique, 1977), and although we did not witness hunting of slow lorises for the pet trade in our study area it was reported for neighbouring villages and is generally common in West Java (Nekaris *et al.*, 2009). We then applied a similar model to the presence of potential predators with one camera trap night as sample unit. For camera trap data we used illumination of the night (number of hours the moon was visible multiplied by moon phase), and we excluded cloud cover. Days without observations or camera traps were excluded. We included an index of effort into the model, consisting of the number of teams observing per night weighted by two to account for a higher viewing angle, plus the number of camera traps working that night. For both models, none of the predictor variables correlated significantly above $r^2 = 0.6$. We used the forced entry method as we had specific predictions about the model (Hill, 2006; Field, 2009). If the odds ratio of a factor is above 1 there is a positive relation between dependent and independent variable.

Results

We collected 7169 5-minute observation points of 12 radio-collared adult individuals, resulting in approximately 600 hours of direct observation and 1036 used data points. The activity budget of all animals per hour can be seen in Figure 1. There was a significant relationship between activity and the different hours of the night (χ^2 = 22.708, df = 9, p<0.007), with animals being less inactive than expected between 19:00 and 20:00.

The logistic regression model with slow loris activity as the outcome variable was highly significant (χ^2 (1) = 116.158, df = 11, p<0.001), with lunar luminosity, humidity, cloud, relative height and the interaction of minimum temperature and moon having a significant effect on whether slow lorises are active or inactive (Table 2). While luminosity and relative height have negative effects on activity, humidity and cloud cover have positive effects. The interaction of minimum temperature and moonlight showed that temperature affected activity during bright nights, but not dark nights. Slow lorises are more active when it is warmer. In dark nights they are equally active in warm and cold nights.

Camera trapping revealed six independent photos of the leopard cat, ten of the Javan ferret badger (*Melogale orientalis* Horsfield 1821), and 14 of the common palm civet. The logistic regression model with predator presence as the outcome variable was not significant (χ^2 (1) = 12.523, df = 7, p<0.085) (Table 4).

Farmers reported to us that domestic dogs sometimes detected and cornered slow lorises. We have never observed any flight or freezing reaction of Javan slow lorises towards common palm civets or leopard cats. In contrast, we have witnessed sub-adults feeding unperturbed by an adult male common palm civet within 5 m distance.

Discussion

Lunar illumination and predation risk

Our model on slow loris activity revealed a negative effect of lunar illumination and relative height on activity, a positive effect of humidity and cloud cover, and an interaction effect of lunar illumination and temperature. Activity was not affected by the number of people observing the slow lorises, neither was an interaction effect with luminosity detected. The predator model was not significant, thus the detection of predators was not affected by moonlight or any climatic factors.

Most primate species increase their activity with increasing lunar illumination (Gursky, 2003; Kappeler and Erkert, 2003; Bearder *et al.*, 2006; Donati and Borgognini-Tarli, 2006; Fernandez-Duque and Erkert, 2006). This can be explained by the high visual orientation in primates and higher effectiveness of foraging and detection of potential predators in bright nights (Gursky, 2003). Instead of hiding in the dark, some lunarphilic primate species additionally use mobbing and warning calls to deter predators and warn conspecifics (Gursky, 2006; Fichtel, 2007, Nash, 2007; Eberle and Kappeler, 2008). In contrast, Javan slow lorises in our study seemed to reduce their activity in brighter nights, as was found for pygmy lorises (Starr *et al.*, 2012) and greater slow lorises (Trent, 1977). We can confirm lunarphobia for Javan slow lorises. Slow lorises thus resemble more the behaviour of other lunarphobic mammals (Prugh and Golden, 2014). This was explained by Starr *et al.* (2012) with the animals' anti-predator behaviour relying on crypsis and concealment, and enhanced by the relatively disturbed and open habitat at our study site.

Although lunarphobic, we did not find any evidence that activity of slow lorises could be negatively affected by human presence, neither was there any apparent relation with the behaviour of

predators. Slow lorises did not engage in more active behaviour like foraging, feeding and travelling in higher and denser canopy, but in contrast are more active in lower heights. Confirmed predators of *Nycticebus* are orang-utans (Utami and van Hooff, 1997), snakes (Wiens and Zitzmann, 1999) hawk-eagles (Hagey *et al.*, 2003), and monitor lizards (Kenyon *et al.*, 2014). Although all of these taxa may not be sympatric with Javan slow lorises, adaptations to such predators may still be responsible for their behavioural responses (Goodman *et al.*, 1993). The African potto (*Perodicticus potto* Mueller, 1766) is comparable to Javan slow lorises in size and ecology and is predated upon by viverrids of relatively small size and by domestic dogs *(Canis lupus* Linnaeus, 1758) (Nash, 2007; Nekaris *et al.*, 2007); pottos showed reactions to viverrids in predation experiments (Charles-Dominique, 1977). Despite presence of potential predators, slow lorises did not show any fear when encountering potential non-human predators. Similar oblivious reactions to potential predators occurred in red and grey slender lorises and in greater slow lorises (Wiens, 2002; Nekaris *et al.*, 2007). Although hunting is the main threat to Javan slow lorises (Nekaris *et al.*, 2009; 2013), the number of observers had no affect on slow loris activity. Lorises may not fear people because they do not perceive people as predators or they are habituated due to the presence of local farmers.

One alternative explanation to predation pressure is a potential higher availability of prey during either moonlit or dark nights. Lang *et al.*, (2005) attributed high activity during dark moon phases of the lunarphobic Neotropical insectivorous bat *Lophostoma silvicolum* Tomes, 1863 to high prey availability of katydids. Foraging depth of Galapagos fur seals (*Arctocephalus galapagoensis* Heller, 1904) followed the moonlight-dependent horizontal migration of fish and squid (Horning and Trillmich 1999). The effect of insect abundance depends on the food preferences of the insectivorous predator. Although these data are not yet available for our field site, it is possible that the higher activity of slow lorises in dark nights follows the higher prey abundance; we are investigating this possibility with future studies.

We suggest that not predator avoidance but alternative factors like higher prey availability cause the slow loris to be more active in darker nights, perhaps due to the extreme morphological adaptations of lorises to avoid predators in the first place. Lorisines rely heavily on crypsis, moving slowly and freezing when feeling threatened (Nekaris *et al.*, 2007). Their fur colour blends in with tree bark and makes animals difficult to detect (Nekaris *et al.*, 2010). Slow lorises are among the few mammal species that are venomous (Alterman, 1995; Hagey *et al.*, 2006; Ligabue-Braun *et al.*, 2012; Nekaris *et al.*, 2013). We are not aware of studies on other venomous mammals with a focus on the influence on moonlight on behaviour. Although uncommon in vertebrates (Pough, 1988), slow lorises may show Muellerian mimicry (Moore, 2012; Nekaris *et al.*, 2013) with Indian cobras (*Naja naja* Linnaeus, 1758). Morphological and behavioural defences against predators can effectively reduce a prey's perception of risk (Stankowich and Blumenstein, 2005), and the combinations of slow lorises' adaptations might be effective enough to make them rather fearless animals when it comes to direct or indirect encounters with potential predators.

Climatic factors

Of the environmental factors, only humidity and cloudiness had a significant independent effect. Different effects of humidity on the activity of animals have been found (positive: Fitzgerald and Bider, 1974; Orrock *et al.*, 2004; Skutelsky, 1996; negative: Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006). Slow lorises become more active with increasing humidity, possibly because of a higher availability of arthropod prey, which also become more active in higher humidity (Fadamiro and Wyatt, 1995). Swifts increase flight height in lower humidity, following flying insects that adapt their flying height to humidity (Shamoun-Baranes *et al.*, 2006). Slow lorises include many flying insects like Coleoptera and Lepidoptera in their diet (Wiens *et al.*, 2006; Starr and Nekaris, 2013). As slow lorises cannot leap or fly, they may be more actively foraging when humidity is high

and insects fly low. Higher percentage of cloud cover contributes to the darkness that is favoured by Javan slow lorises. As the temperature at our study site can drop to about 10 °C, it is likely that temperature would have affected the activity of Javan slow lorises. Although we could not find an independent effect of temperature, we detected an interaction effect of luminosity and temperature in Javan slow lorises, just like for pygmy lorises (Starr *et al.*, 2012). Indeed, during these inactive bouts, Javan slow lorises, like pygmy lorises, might not move for hours at a time. Many small endotherm species show heterothermy (Heldmeier and Ruf, 1992; Heldmaier *et al.*, 2004), including several nocturnal primates such as lemurs of the family Cheirogaleidae and lesser bushbabies (*Galago moholi* Smith, 1836) (Schmid, 2000; Smit *et al.*, 2001; Dausmann *et al.*, 2005; Schuelke and Ostner, 2007; Nowak *et al.*, 2010). *Nycticebus* spp. are able to enter torpor (Whittow *et al.*, 1977; Xiao *et al.*, 2010). We have already found evidence for torpor in one animal at our study site (Rode-Morgano and Nekaris, unpub. data) and we are further investigating through physiological measurement if animals at our site regularly enter torpor during cold temperatures. We attributed the positive effect of higher humidity on activity to an adaptation to the activity of flying insect prey. Potential predators showed no preference for dark or bright nights and we could not detect an effect of climate factors on their activity.

Conclusion

Nash (2007) rightfully stressed that crypsis and predation are not unitary phenomena but interact in complex ways. Most primate species are lunarphilic, but slow lorises seem to be the exception from that rule and decrease activity in bright moonlight (lunarphobia) like most other mammals. A higher activity when cloud cover is higher may contribute to this behaviour. Javan slow lorises seem to be indifferent to potential predators and do not shift their activities into more covered habitat. We suggest that lunarphobia in slow lorises is not due to an increased perceived predator risk, but due to other factors like lower availability of prey species in moonlit nights. Additionally, slow lorises may

be well-adapted to avoid or defend against predators by crypsis, venom and mimicry, and thus, do not need to be afraid in the dark.

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Figure captions:

Figure 1: Activity budget per hour for 12 adult Javan slow lorises. N = 915. Data points were at least one hour apart. Sample sizes for the respective hours are given in brackets. Inactive behaviour is indicated by the category “rest and sleep”.

Table captions:

Table 1: Reactions of some animal species towards moonlight, and adaptive explanations.

Table 2: Results of the logistic regression model with activity of Javan slow lorises as a binary outcome variable

Table 3: Results of the logistic regression model with presence of predators as a binary outcome variable